

COURTSHIP, MATING AND POST-OVIPOSITION BEHAVIOUR OF *HYPOCHILUS POCOCKI* PLATNICK (ARANEAE, HYPOCHILIDAE)

K. M. CATLEY

Catley, K.M. 1993 11 11: Courtship, mating and post-oviposition behaviour of *Hypochilus pococki* Platnick (Araneae, Hypochilidae). *Memoirs of the Queensland Museum* 33 (2): 469-474. Brisbane. ISSN 0079-8835.

Courtship and mating in *Hypochilus pococki* Platnick is described for the first time for any member of the superfamily Hypochiloidea. Five phases of male behaviour are recognised; pre-courtship, non-contact courtship, contact courtship, copulation and post-copulatory behaviour. Chemotactic stimulation seems to be the prime releaser of male courtship behaviour which involves web-tugging, mutual leg-stroking and female guarding. Post-oviposition behaviour is described and the role of a previously undescribed sheet web, constructed by females after oviposition as well as early instar spiderlings, is discussed in terms of its phylogenetic implications. □ *Hypochilus*, courtship, phylogenetics, sexual selection, web construction.

K.M. Catley, Department of Biology, Western Carolina University, Cullowhee, North Carolina 28723, USA; Present address: Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0999, USA; 13 October, 1992.

The significance of undertaking ethological studies of spiders in the family Hypochilidae stems from the phylogenetic position of the family as a relic taxon at the base of the Infraorder Araneomorphae (Platnick, 1977; Forster *et al.*, 1987). Diagnosis of behavioural units that are used in such processes as web construction (Coddington, 1986) and courtship (Platnick, 1971; Helversen, 1976; Coyle and O'Shields, 1990) may prove useful in future phylogenetic analysis. This paper describes the courtship and mating behaviour of *Hypochilus pococki* in the laboratory and attempts to recognise potentially informative behavioural sequences. Egg sac construction is also described and attention drawn to a previously undescribed silk construct, a 'veil web' built by post egg-laying females as well as early instar spiderlings. Apart from one incomplete observation by Fergusson (1972) of mating in *Hypochilus thorelli* Hoffman (= *Hypochilus pococki*), this is the first detailed description of reproductive behaviour for any member of the superfamily Hypochiloidea.

The genus *Hypochilus* comprises five species confined to the Southern Appalachian highlands of eastern North America, two species from central and northern California and one from central Colorado. Two additional species, one from New Mexico and the other from the San Bernardino Mountains of southern California will soon be described (Catley in prep.). These haplogyne cribellate spiders build characteristic 'lampshade' webs on rock surfaces often close to running water. All species appear to be allopatric

and exhibit an interesting pattern of disjunct endemism (Catley, 1991, Huff and Coyle, 1992). Males moult to maturity later than females, typically appearing in early August. They move extensively (presumably in search of females) and do not associate with penultimate females, suggesting that there is no first male sperm precedence (Eberhard *et al.* in press).

MATERIALS AND METHODS

Despite extensive day and night observation during 1990 and 1991, no courtship or mating behaviour was observed in the field. *Hypochilus* can be very difficult to maintain in the laboratory; they are affected adversely by changes in humidity and only occasionally can they be persuaded to construct a web, making feeding problematical. Following several unsuccessful attempts to establish a mature female in the laboratory, a single specimen collected in July 1990 from Wolf Creek watershed, Cullowhee, Jackson County NC, established a web in a 50x30cm glass tank. The tank was furnished with a sloping wooden framework (45° angle) covered with sandpaper to simulate an overhanging rock ledge. The floor was covered with vermiculite to a depth of 5cm and was kept very moist.

After the female attacked and killed the first male introduced into the arena, she was allowed to feed for a period of one week. The second male was introduced on August 28 1990 and a total of 7 hours 47 mins of male/female encounters were filmed using a Panasonic WV-D5000 video re-

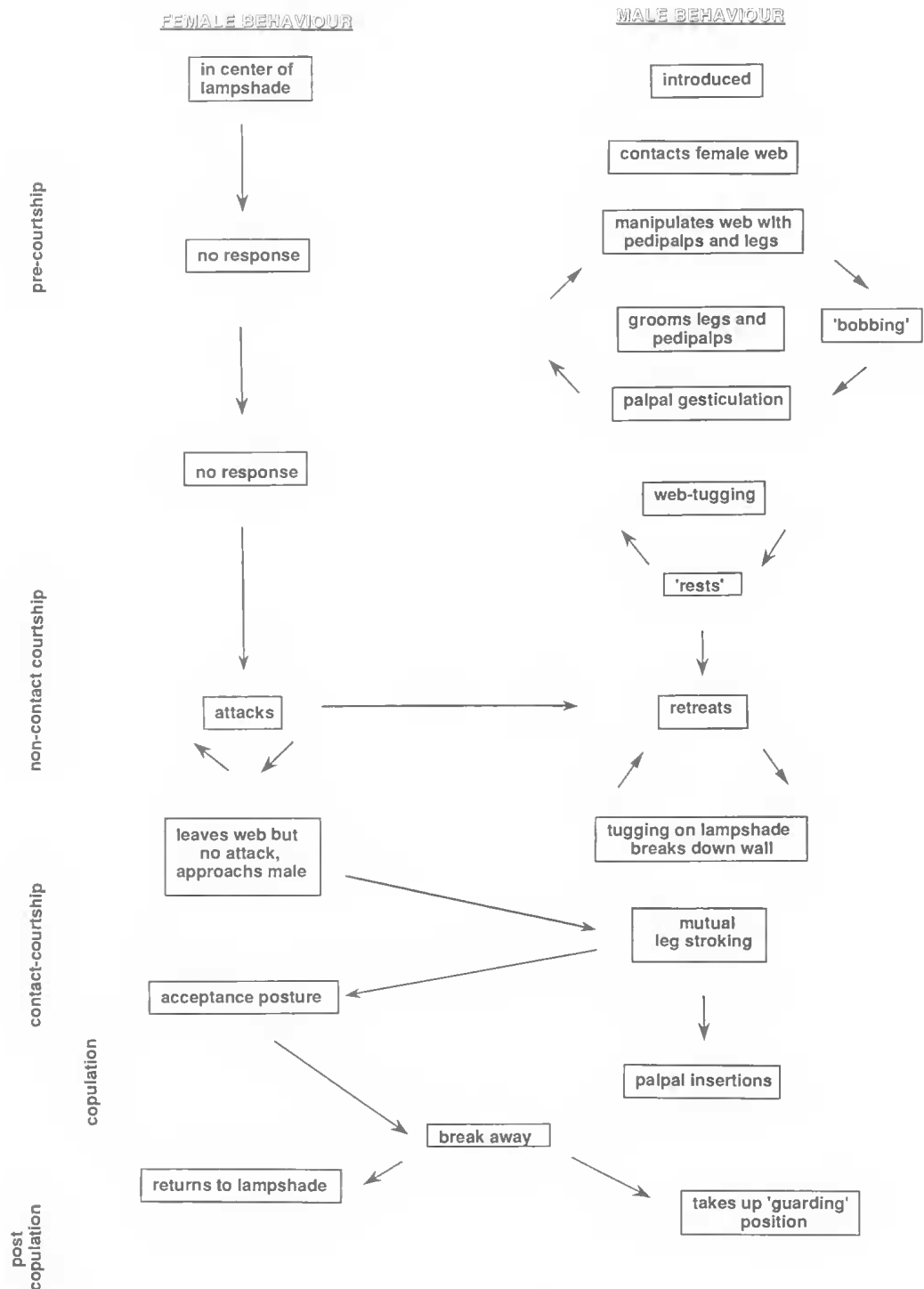


FIG. 1. Sequence of courtship and mating behaviour in *Hypochilus pococki* formulated from encounters in the laboratory involving two males and a single female (see text for explanation).

corder fitted with a Micro-Nikkor 55mm close-up lens. Sessions were annotated by verbal comments recorded through the audio channel of the video camera. Data analysis was achieved using slow motion and freeze frame functions of a VCR.

RESULTS

The description of courtship and mating presented here is a composite derived from laboratory observations of only two males and a single female and therefore may not be representative.

Male courtship behaviour can be divided into five distinct phases: pre-courtship, non-contact courtship, contact courtship, copulation and post-copulation (Fig. 1). The following behavioural units were diagnosed.

MALE BEHAVIOURAL UNITS

PRE-COURTSHIP

Leg and pedipalpal grooming. Within a few minutes of a male being introduced into the arena, the legs and pedipalps were used to manipulate female silk. A web constructed by the same female but which had been abandoned for several weeks elicited the same response. Rubbing the tarsi and metatarsi of legs 1, 2 and 3 together, as well as drawing them and the pedipalps between the open chelicerae (and presumably the endites) occurred immediately after the first and subsequent encounters with the female web. The pedipalps were rubbed vigorously across the silk for extensive periods, this was followed either by drawing them through the mouthparts, as described above, or by rapid pedipalpal gesticulations.

Bobbing. Flexing of the legs resulted in the whole body moving up and down relative to the substrate. Bobbing is often interspersed between sessions of leg and pedipalpal grooming.

NON-CONTACT COURTSHIP

Web-tugging. The male pulled on the cribellate lampshade web of the female with his first pair of legs. Such actions, repeated in bouts lasting 3-7 seconds interspersed with periods of inactivity lasting from 5 secs. to several mins., can result in the side wall of the lampshade being partially destroyed.

CONTACT COURTSHIP

Leg-stroking. The female eventually left the

web as a result of male tugging and approached the male, waving her front pair of legs. The male held his ground (unlike previous female approaches which appeared aggressive and from which the male quickly withdrew). A long session of mutual leg-stroking followed, involving mainly legs one and two. The male maintained a constant, very rapid stroking of the female's legs (mainly metatarsi and tibiae) and body as she appeared to become progressively more cataleptic, and eventually assumed the acceptance posture. This stroking session lasted for 3 mins. 12 secs—more than twice the period of copulation itself.

COPULATION

Palpal insertions. Following mutual leg-stroking the female oriented her abdomen at 45° to the substrate and adopted a semi-cataleptic acceptance posture. The male faced the female and advanced, with pedipalps fully extended, to a position where his dorsal cephalothorax was adjacent to the female's sternum (Fig. 2). It was not entirely clear whether or not the male tapped on the female's genital area with his palps prior to insertion as described for some araneids (Robinson and Robinson, 1980). Such apparent tapping may simply be attempts to locate the opening to the bursa copulatrix.

The palps were inserted alternately, the right followed by the left, each insertion lasted 3-10 seconds with the whole insertion sequence lasting 1 min. 22 secs. To achieve insertion from this position requires that the palpal organ be twisted through 90° at the same time as the pedipalp is straightened. The copulatory phase ended abruptly when the female broke away from the male, who was immediately pursued some distance from the web. At no time during courtship or mating was the male observed to lay down silk.

POST-COPULATION

'Guarding' posture. After copulation, the male, after a brief period of palpal grooming, took up a characteristic position close to the female, often touching her. His legs were extended parallel to the substrate, with the first three pair directed anteriorly, and the fourth pair directed posteriorly. The first pair of legs were held in such a position such that the femora were at 30° to the longitudinal axis of the prosoma, while the remaining podites tended to converge distally over the female. This seems to be a characteristic position seen often in the field. It was maintained

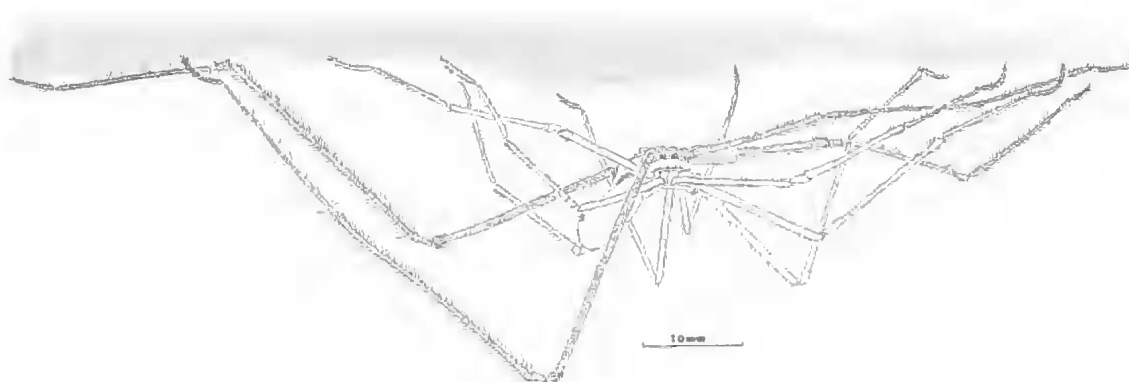


FIG. 2. Mating position of *Hypochilus pococki* (for the sake of clarity not all male appendages are illustrated).

for 2.5 hours after which the female attacked and badly injured the male.

FEMALE BEHAVIOURAL UNITS

NON-CONTACT

Attack. The female failed for long periods to show any response to the male's web-tugging but did eventually respond by rushing out of the lampshade and pursuing him. Three attacks appeared in earnest, with the male withdrawing rapidly. The fourth response was instigated more slowly (with reduced speed and vigour); this change in 'intent' appeared to be sensed by the male, who did not retreat. This encounter led directly to contact courtship and copulation (Fig. 2).

CONTACT COURTSHIP

Leg stroking. See male behaviour.

COPULATION

Acceptance posture. A semi-cataleptic position with the abdomen held at 45° to the substrate (Fig. 2) occurring after contact courtship (extensive leg stroking) with the male.

POST-COPULATION

Egg laying ethology. Twenty days after copulation, the female laid eggs and constructed an egg-sac. First a saucer-shaped disc of pink silk was laid down onto which the eggs were deposited. This was then closed up to form a flattened sphere. The pink colour of the silk has been corroborated by several observations in the field, however, when the egg-sac is ready to be covered in cryptic material its colour is off-white. A second egg-sac was produced on October 4, followed by a much smaller egg-sac on October

17, and the final egg-sac was constructed on November 6. Each was suspended from the framelines of the web while particles were incorporated in the outer layer of the egg-sac. This involved the spider descending to the substrate and carrying pieces of vermiculite back to the web in her chelicerae (in the field egg cases are covered with particles of moss or lichen (Ferguson, 1972; pers. obs.).

Two egg-sacs were 'screened in' by a particular type of sheet web not previously described for *Hypochilus*. Observations from the field show that a similar 'veil web' is also constructed by early instar spiderlings (Catley, 1991). The silk is of very different appearance from either framework or cribellate silk and appears as a dense, finely woven sheet. Its purpose, either as a vertical 'veil' in front of egg-sacs (typically those suspended in a fissure in the rock), or as a barrier underneath which a number of very early instar spiderlings build their regular prey catching lampshade webs, may be protective.

DISCUSSION

The function of courtship in spiders may be most simply expressed as: alerting the female to the presence of the male, the possible suppression of female predatory behaviour and stimulation of the female to accept copulation. Variations on this basic theme have been voiced by several authors including Bristowe (1958), Crane (1949) and Platnick (1971); most expand the concept to include elements of species specific recognition, advertisement of sexual availability and the functioning of a releaser system. Other components which may also be important are male behavioural elements designed to ensure his post-copulation survival.

Accounts of courtship and mating in other more primitive spider taxa are scant, but include information on the Mesothelae: Liphistiidae, *Hep-tathela* (Haupt, 1977); Mygalomorphae: Nemesiidae (Buchli, 1962); Atypidae (Clark, 1969); Dipluridae (Coyle and O'Shields, 1990). Whereas behavioural observations for spiders in the Araneoclada are available from Bristowe (1941, 1958) various families, Crane (1949) for salticids, and Robinson and Robinson (1978, 1980) for araneids, this account of courtship and mating in *Hypochilus* is the first to be published for any lower (non-Araneoclada) araneomorph spider.

The courtship and mating repertoire of *Hypochilus* is relatively underived and given the families' phylogenetic position the behavioural units which comprise it may be hypothesised to represent the plesiomorphic condition of araneomorph reproductive behaviour in general. Given a larger data base within the Araneomorphae, comparison of behavioural characters will allow correct polarity decisions to be made and the resulting data set, combining both morphological and ethological characters, should provide a more stringent test of phylogeny.

Leg and pedipalpal grooming behaviours performed by the male upon contact with the female web may be indicative of the occurrence of female pheromone on the web. Such pre-contact encounters were necessary to release web-tugging behaviour in these observations ($n=4$) and is consistent with Platnick's (1971) hypothesis that chemotactic stimuli are prime releases of male courtship behaviour in haplogyne spiders. It has been suggested that the longer anterior legs of male *Hypochilus* confer superior mobility when locating females (Fergusson, 1972; Eberhard *et al.* in press). However, such pronounced sexual dimorphism may have had its origin in courtship behaviour. The extreme length of the first legs, by maximising the distance between male and female during web-tugging, should increase the male's chance of surviving female attacks. Such interactions may also provide an opportunity for sexual selection by female choice to occur (Eberhard, 1985), the female testing male 'fitness' by repeated attacks.

Contact courtship was initiated when the female eventually left the lampshade and approached the male. Such behaviour may not however be typical. Fergusson (1972) reported that in the one encounter he observed the male scrambled into the lampshade with the female. The long period of mutual leg-stroking may play

a role in placating the female, resulting in her adopting the acceptance posture. It may well be homologous with the 'leg fencing' behaviour seen in some diplurid spiders (Coyle and O'Shields, 1990).

Copulation was achieved in the mating position (Fig. 2; position 1 of Kaston, 1981). Alternate palpal insertions, as observed in *Hypochilus*, should be considered plesiomorphic when encountered in other araneomorph spiders (using *Hypochilus* as an outgroup) and as apomorphic when palps are inserted simultaneously. Simultaneous palpal insertion has been documented in the following families, Dysderidae, Segestriidae, Onnopidae, Scytodidae and Pholcidae (Bristowe, 1958) but appears not, as Bristowe concluded, to be plesiomorphic for the Araneoclada. Simultaneous insertion may well prove to be a synapomorphy for the higher haplogynes, Dysderoidea plus 'Scytodids' (Coddington and Levi, 1991).

The post-copulatory position taken up by the male is believed to represent a guarding posture. *Hypochilus pococki* males have been shown conclusively not to associate with penultimate females (Eberhard *et al.* in press). Hence, that the numerous occasions when males were found in this position in the field, suggest that they represent in fact, post-mating situations, and that the male was most likely guarding the female and thus his chance of paternity.

The implications of the 'veil' web produced by the female following egg-sac construction require further comment. *Hypochilus* egg-sacs are superbly cryptic and most are not concealed by such a 'veil' web (Shear, 1969; Fergusson, 1972; Catley, 1991). The behaviour of some females in concealing egg-sacs might have primitively represented a selective advantage from vertebrate or hymenopteran predation.

Accepting the cladistic hypothesis of Forster *et al.* (1987) on the relationships of the Hypochiloidea and Austrochiloidea, data on sheet web construction in these taxa suggests that the lampshade web of *Hypochilus* is autapomorphic. *Ectatosticta davidi* (Simon), the sister taxon of *Hypochilus*, constructs a sheet web (Li and Zhu, 1984) as do all known members of Austrochilidae (Forster *et al.*, 1987). Ontogenetic evidence, based on the observation that very early instar spiderlings also construct a sheet web (Catley, 1991), also supports this hypothesis and lends some weight to the suggestion that the plesiomorphic web construct of araneomorph spiders was the sheet web.

ACKNOWLEDGEMENTS

Grateful thanks are due to Dr. Frederick Coyle for the loan of video recording equipment, Rudolf Meier for help with translations and Dr. William Shear for his useful comments on an early draft of the manuscript. I should like to acknowledge financial support from the Organising Committee of the XII International Congress of Arachnology, the Graduate School of Cornell University and the Grace Griswold Fund which allowed me to attend this Congress.

LITERATURE CITED

- BRISTOWE, W.S. 1941. The Comity of Spiders. vol. II. (Ray Society: London).
1958. The World of Spiders. (Collins: London).
- BUCHLI, H. 1962. Note préliminaire sur l'accouplement des araignées mygalomorphes *Nemesia caementaria*, *Nemesia dubia* et *Pachylomerus piceus*. Vie et Milieu 13: 167-178.
- CATLEY, K.M. 1991. The phylogenetic relationships of the species of the lampshade spider genus *Hypochilus* (Araneae, Hypochilidae). (Unpublished Masters thesis, Western Carolina University).
- CLARK, D. J. 1969. Notes on the biology of *Atypus affinis* Eichwald. Bulletin of the British Arachnological Society 1: 36-39.
- CODDINGTON, J. A. 1986. The monophyletic origin of the orb-web. Pp. 319-363. In Shear, W. A. (ed). 'Spiders. Webs, behavior, and evolution'. (Stanford University Press: Stanford, California).
- CODDINGTON, J. A. & LEVI, H.W. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22: 565-92.
- COYLE, F. A. & O'SHIELDS, T. C. 1990. Courtship and mating behavior of *Thelechoris karschi* (Araneae, Dipluridae), an African funnel web spider. Journal of Arachnology 18: 281-296.
- CRANE, J. 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. Zoologica 34: 159-214.
- EBERHARD, W. G. 1985. Sexual selection and animal genitalia. (Harvard University Press: Cambridge).
- EBERHARD, W. G., GUZMAN-GOMEZ, S. & CATLEY, K. M. (in press). Correlation between spermathecal morphology and mating systems in spiders. Biological Journal of the Linnean Society.
- FERGUSON, I. C. 1972. Natural history of the spider *Hypochilus thorelli* Marx (Hypochilidae). Psyche 79: 179-199.
- FORSTER, R.R., PLATNICK, N.I. & GRAY, M.R. 1987. A review of the spider superfamilies *Hypochiloidea* and *Austochiloidea* (Araneae, Araneomorphae). Bulletin of the American Museum of Natural History 185: 1-116.
- HAUPT, J. 1977. Preliminary report on the mating behaviour of the primitive spider *Heptathela kimurai* (Kishida) (Araneae, Liphistiomorphae). Zeitschrift für Naturforschung 32: 312-314.
- HELVENSEN, O. VON 1976. Gedanken zur Evolution der Paarungsstellung bei den Spinnen (Arachnida, Araneae). Entomologica Germanica 3: 13-28.
- HUFF, R. P. & COYLE, F. A. 1992. Systematics of *Hypochilus sheari* and *Hypochilus coylei*, two southern Appalachian lampshade spiders (Araneae, Hypochilidae). Journal of Arachnology 20: 40-46.
- KASTON, B.J. 1981. Spiders of Connecticut. State Geological and Natural History Survey of Connecticut. Department of Environmental Protection. Bulletin 70.
- LI, ZHONSHAN & ZHU, CHAUNDIAN, 1984. *Ec-tatosticta davidi* (Simon, 1888) of China (Araneae: Hypochilidae). Journal of the Bethune Medical University 10(5): 510 (in Chinese).
- PLATNICK, N. I. 1971. The evolution of courtship behaviour in spiders. Bulletin of the British Arachnological Society 2(3): 40-47.
1977. The hypochiloid spiders: a cladistic analysis with notes on the Atypoidea (Arachnida, Araneae). American Museum Novitates 2627: 1-23.
- ROBINSON, M.H. & ROBINSON, B. 1978. The evolution of courtship systems in tropical araneid spiders. Symposia of the Zoological Society of London 42: 17-29.
1980. Comparative studies of the courtship and mating behavior of tropical araneid spiders. Pacific Insects Monograph 36: 1-218.
- SHEAR, W. A. 1969. Observations on the predatory behavior of the spider *Hypochilus gertschi* Hofman (Hypochilidae). Psyche 76: 407-417.